

Chapter 1

Introduction: Young Approaches to Animal Evolution



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For centuries, scientists have tried to understand animal evolution. In recent years, a series of emerging technologies, such as high-throughput sequencing of genomic and transcriptomic data, molecular tools to manipulate gene function, microscopy techniques to image living cells, tissues, and embryos, and computational methods to analyse and model biological processes, are revolutionising all areas of biology—from the analysis of molecules to ecosystems. Evolutionary developmental biology (“EvoDevo”) has dramatically benefited from this new technical paradigm, crystallising as a discipline, and setting the foundations for a more comprehensive and integrative understanding—and study—of animal development and evolution. Thus, our aim with this book is to showcase this change, incorporating different research and conceptual perspectives, and trying to make the current view of animal development and evolution accessible to all.

Before delving into the book’s contents, we briefly review a topic that is at the core of all evolutionary studies—the phylogenetic relationships between animal groups.

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1.1 A Molecular Phylogenetic Revolution

High-throughput sequencing has arguably been the greatest game changer in animal evolutionary biology. For decades, comparative morphology dominated the study of animal evolution. Morphological and developmental similarity were criteria to define phylogenetic relationships among animal groups and thus to explain the origin and diversification of animal lineages and ground plans (Ax 1996; Haeckel 1874; Hyman 1951b; Remane 1950; Salvini-Plawen 1978). It is still evident today that some of the core concepts—but also misconceptions—of modern animal evolutionary developmental biology stem from morphological phylogenetic interpretations that often date back to more than a century ago (Fig. 1.1; see, e.g., Chaps. 4 and 7). However, the development of statistical and computational algorithms that use molecular information (e.g. amino acid and nucleotide sequences) as character traits for phylogenetic reconstruction (Hennig 1966; Yang and Rannala 2012), combined with advances in sequencing technologies that allowed generating massive amounts of molecular data in a fast and affordable manner (Goodwin et al. 2016), has transformed the study and interpretation of animal evolution. On the one hand, high-throughput sequencing has allowed us to study morphological and developmental processes at levels of biological complexity that were barely imagined just a few decades ago (see, e.g., Chaps. 6, 9, and 10). On the other hand, the use of molecular data to infer phylogenetic relationships has made possible to dissociate phylogenetic reconstruction from trait evolution, overcoming the circular reasoning resulting from employing morphological data to construct phylogenies that were then used to infer the evolution of animal morphology. Indeed, molecular phylogenetics has shaken the animal tree of life (Fig. 1.2) (Aguinaldo et al. 1997; Cannon et al. 2016; Dunn et al. 2008; Feuda et al. 2017; Halanych et al. 1995; Philippe et al. 2005, 2011; Ruiz-Trillo et al. 1999), and even when there are still key contentious issues, it has forced us, evolutionary biologists, to rethink many of the long-standing views on how animals originated and diversified.

It is today widely accepted that all animals share a common ancestor—i.e. are a monophyletic group—and that unicellular choanoflagellates are their closest living relatives (Lang et al. 2002; Wainright et al. 1993). While a close affiliation of choanoflagellates and animals had been proposed already in the mid-1800s based on morphological similarities (James-Clark 1866), it is perhaps more remarkable that molecular phylogenetics is placing a growing number of unicellular organisms that were formerly loosely considered within the “protists” as animal relatives (Lang et al. 2002; Ruiz-Trillo et al. 2008; Torruella et al. 2012). This has led to the establishment of Holozoa (Lang et al. 2002), a broader monophyletic group comprising multicellular animals and all their unicellular relatives, which has been key in defining a new narrative of the earliest steps of animal evolution, in particular at the level of the genomic and epigenomic changes that potentially facilitated the evolution of animal multicellularity (see Chap. 2) (Sebé-Pedrós et al. 2017).

It is, however, paradoxical that all the advances in identifying the deepest unicellular roots of animals have occurred simultaneously to the arrival of a still

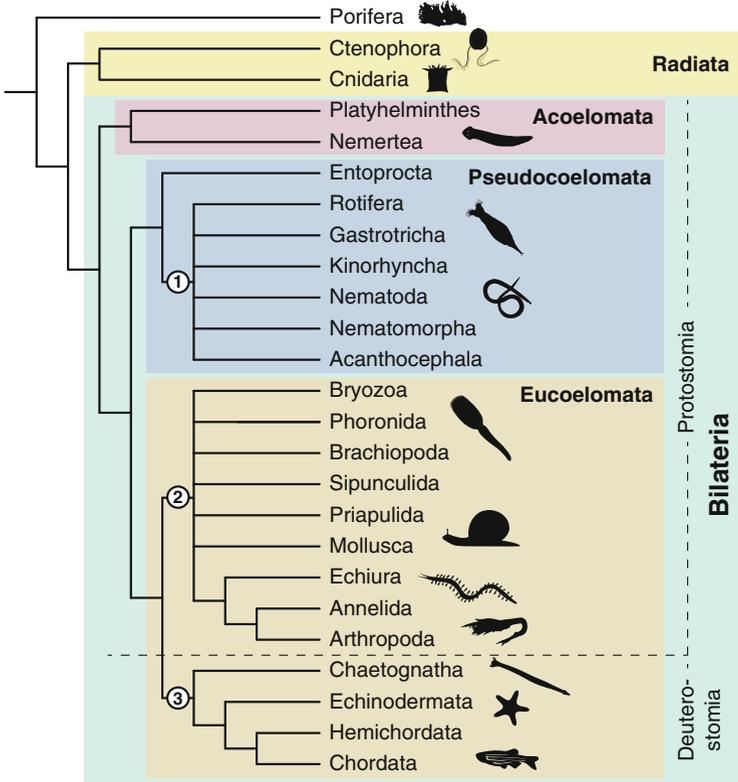


Fig. 1.1 Traditional animal phylogeny based on morphological characters. Animal phylogeny according to Hyman (1951a). Body symmetry divides animals into Porifera (no symmetry), Radiata (radial symmetry), and Bilateria (bilateral symmetry). The presence/absence of internal body cavities subdivide Bilateria into Acoelomata (no internal body cavity), Pseudocoelomata (internal body cavity lined by the body wall), and Eucoelomata (internal body cavity lined by a mesoderm-derived tissue). In addition, Pseudocoelomata includes one large grouping, Aschelminthes (1), and Eucoelomata is subdivided according to the mode of coelom formation, namely Schizocoela (2) and Enterocoela (3). The fate of the blastopore also subdivides Bilateria into a “lower” polyphyletic Protostomia and a “higher” Enterocoela. We thank Michelle Site for the silhouettes of a nematode and an annelid, Noah Schlottman for the silhouette of a planarian, and *PhyloPic* database for the remaining silhouettes

ongoing debate on the earliest radiations of multicellular animals, in particular regarding the phylogenetic position of Porifera—sponges—and Ctenophora—comb jellies (Dunn et al. 2015; Halanych 2015; Halanych et al. 2016; Jékely et al. 2015; Pisani et al. 2016). Traditionally, sponges were regarded as the sister taxon to all remaining animals (Fig. 1.1) (Ax 1996; Haeckel 1874; Hyman 1951a), a view relying heavily on comparative morphology and often on a simple-to-complex assumption of animal evolution (Halanych 2015). While this scenario has received support from several modern phylogenetic analyses (Feuda et al. 2017; Pick et al.

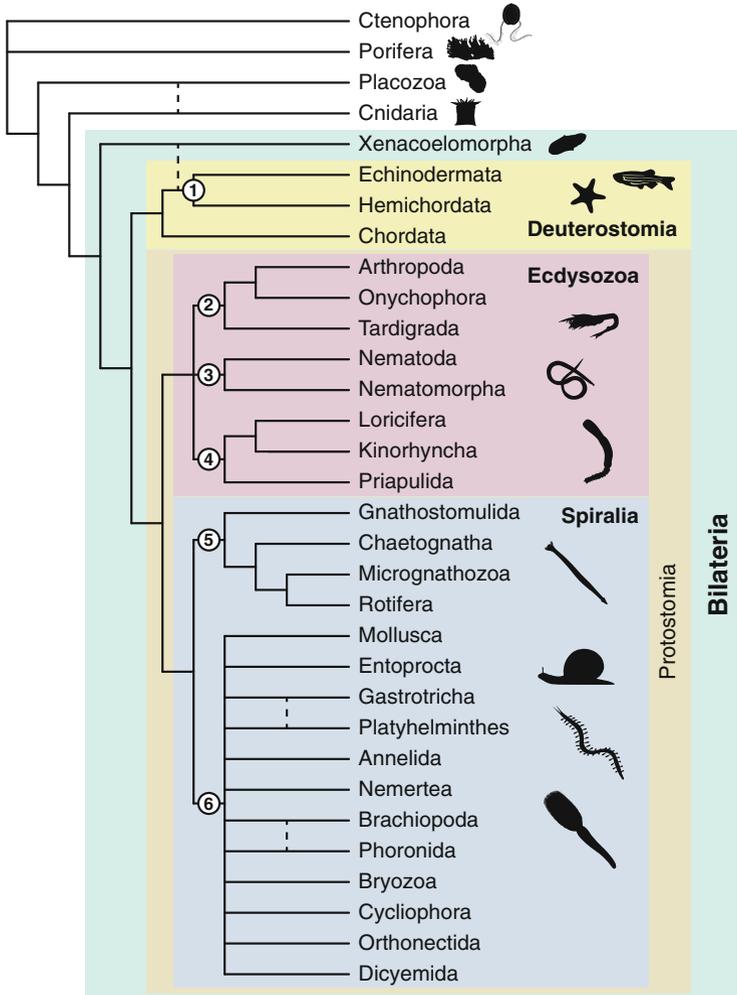


Fig. 1.2 Modern animal phylogeny based on molecular data. Animals are a monophyletic clade. However, whether Porifera or Ctenophora are the sister lineage to the rest is still contentious. Cnidarians are the sister taxon to Bilateria, and there is some debate regarding the position of Placozoa. Bilateria is divided into three major lineages: Deuterostomia, Ecdysozoa, and Spiralia. The internal relationships within these groups are still debated, yet there are some well-supported and stable clades, such as Ambulacraria (1), Panarthropoda (2), Nematoida (3), Scalidophora (4), Gnathifera (5), and Lophotrochozoa (6) (sensu (Marlétaz et al. 2019)). See the main text for further clarifications and references. We thank Michelle Site for the silhouettes of a nematode and an annelid, and *PhyloPic* database for the remaining silhouettes

2010; Pisani et al. 2015), it has also been suggested that comb jellies could occupy the position of sponges as sister taxon to all remaining animals (Dunn et al. 2008; Moroz et al. 2014; Ryan et al. 2013; Whelan et al. 2015, 2017). Contrary to sponges, comb jellies have neurons, muscle cells, a functional through-gut, body symmetry,

and elaborated behaviours (Hyman 1951a). Therefore, placing ctenophores as one of the earliest branching lineages in the animal tree of life imposes novel interpretations of the evolution of multiple morphological traits (see, e.g., Chap. 8), which imply that either sophisticated cell types and morphological and developmental features can evolve convergently several times or were ancestral and subsequently got lost in the lineage leading to sponges. As striking and stimulating as this debate can be, it also highlights the limitations of modern molecular phylogenetic approaches to resolve some of the interrelationships of extant animals, in particular in situations where different analytical strategies offer conflicting results (King and Rokas 2017; Shen et al. 2017).

The Porifera–Ctenophora phylogenetic controversy has not been the only recent dispute dominating the study of animal diversification at macroevolutionary time-scales. The monophyly of bilaterally symmetrical animals—i.e. Bilateria—and its sister-taxon relationship with Cnidaria—sea anemones, corals, and jelly fishes—is very well supported by both morphological and molecular data (Dunn et al. 2014). However, the inclusion of new species, genome-wide data, and novel analytical strategies has challenged the position of Placozoa—a group of flat animals lacking muscles, neurons, and gut—as sister taxon to the clade Cnidaria + Bilateria and instead suggested a closer affinity of this group to Cnidaria (Laumer et al. 2018). Under this scenario, many homologous characters between Cnidaria and Bilateria that are missing in Placozoa, such as neurons and gastrulation dynamics (see Chaps. 5, 7, and 8), evolved earlier than previously thought in animal evolution and probably represent secondary losses of the lineage leading to placozoans.

Similarly, the contentious phylogenetic position of Xenacoelomorpha—a group of worm-like bilaterian animals lacking a through-gut and excretory organs, and with a diffuse nerve net as primitive neuroanatomy—still influences scenarios for the evolution of Bilateria (Cannon et al. 2016; Philippe et al. 2011; Rouse et al. 2016; Ruiz-Trillo et al. 1999). Traditionally placed within Platyhelminthes, which were regarded as the sister taxon to all remaining bilaterians (Fig. 1.1) (Hyman 1951b), molecular phylogenies soon segregated acoelomorph worms from Platyhelminthes; the former remained as sister taxon to Nephrozoa—the remaining bilaterian animals, which all share the presence of excretory organs—and the latter became more deeply nested in the bilaterian phylogeny (Fig. 1.2) (Ruiz-Trillo et al. 1999). While the vast majority of molecular phylogenetic analyses support today separating acoelomorph worms from Platyhelminthes, which is indeed congruent with morphological and developmental data (Ax 1996; Boyer et al. 1996; Ruiz-Trillo et al. 1999), the exact position of xenacoelomorphs—acoelomorph worms plus xenoturbellid worms—has become a matter of debate. The more traditional sister-to-Nephrozoa position (Cannon et al. 2016) has been challenged by analyses that place xenacoelomorph worms as sister taxon to echinoderms and hemichordates either within Deuterostomia (Philippe et al. 2011), or as sister group to the remaining bilaterians (Marlétaz et al. 2019). But as in the Porifera–Ctenophora debate, differences in analytical strategies significantly influence the phylogenetic positioning of xenacoelomorph worms, and thus, it might be necessary to turn to other characters, such as rare

genomic changes, to improve and eventually resolve our understanding of the earliest steps of Bilateria evolution.

The advent of molecular phylogenetics also transformed the interrelationships between major bilaterian groups. To the already mentioned division of Platyhelminthes *sensu stricto* and Xenacoelomorpha, phylogenetic arrangements based on the presence/absence of morphological characters, such as the Coelomata/Pseudocoelomata/Acoelomata classification based on the type of internal body cavities, have been superseded by a robust and stable arrangement in three major bilaterian lineages, namely Deuterostomia, Ecdysozoa, and Spiralia (Fig. 1.2) (Aguinaldo et al. 1997; Dunn et al. 2008; Halanych et al. 1995). Although the internal relationships between the major animal clades comprising Ecdysozoa and Spiralia remain controversial (Borner et al. 2014; Giribet and Edgecombe 2017; Kocot et al. 2017; Laumer et al. 2015; Marlétaz et al. 2019; Struck et al. 2014), this new phylogenetic framework has had profound implications in the interpretation of how morphological and developmental traits evolved in Bilateria. Internal body cavities, metameric segmentation, gastrulation modes, cleavage patterns, and trunk neuroanatomies are some of the character complexes traditionally used to explain animal evolution that exhibit today a story of convergence and innovation (Martín-Durán et al. 2016, 2018; Roy and Irimia 2008a, b; Vellutini and Hejnal 2016; Vellutini et al. 2017), which instead of blurring our understanding of how bilaterian animals diversified represent an open window to investigate the mechanisms that allow the evolution of similar phenotypic outcomes from separate phylogenetic, and thus genotypic, starting points.

The consequences and opportunities of the molecular phylogenetic revolution experienced in animal evolutionary developmental biology extend well beyond the few and very general changes described in the paragraphs above. The internal phylogenetic relationships of nearly all major animal groups have been updated in one way or another, which has forced us to revisit traditional concepts on how particular animal groups evolved and radiated. Perhaps the most illustrative case is Chordata, where urochordates and not cephalochordates emerged as the sister taxon to vertebrates (Philippe et al. 2005). However, the impact of this revolution extends also beyond the pure study of animal interrelationships, because it has created a common and rather stable experimental and conceptual evolutionary framework. A revolution that, as we aim to show with this book, has a strong influence in the way we approach and explain animal biology and evolution at all levels, from molecules (see Chaps. 2, 9, and 10) and fossils (see Chap. 3) to embryos (see Chaps. 4, 5, 6, 7, and 8) and mathematical models (see Chaps. 11, 12, and 13).

1.2 The Structure of This Book

We have organised the chapters into four parts that reflect different but complementary views about animal evolution. The first part is entitled “Animal Origins” (Chaps. 2 and 3) and addresses how novel sources of evidence from unicellular

organisms and fossils are changing the conventional views about the onset and diversification of animals. The second and largest part of this book is entitled “The Developmental View of Animal Evolution” (Chaps. 4, 5, 6, 7, and 8) and discusses the relation between development and evolution as well as the origins of key metazoan traits, such as germ layers and nervous systems. The third part, “The Genomic View of Animal Evolution” (Chaps. 9 and 10), explores how changes in regulatory interactions between genes and other epigenetic mechanisms can lead to morphological evolution. Finally, the last part, entitled “Theoretical Approaches to Animal Evolution” (Chaps. 11, 12, and 13), tackles the importance of modularity, individuality, and computational modelling to understand animal development and evolution.

Opening the part “Animal Origins”, Mendoza and Sebé-Pedrós approach in Chap. 2 a question that stayed largely untested for more than a century—how did animals first evolve from unicellular ancestors? The evolution of metazoan multicellularity had a profound influence on the history of life on Earth. However, the key features and evolutionary steps that led to this major transition have remained rather speculative until the recent advancements in (phylo)genomics. These tools have enabled the discovery of extant unicellular organisms closely related to metazoans and deeper insights into their molecular and cellular biology, thus providing at last more solid phylogenetic and biological grounds to test hypotheses about the origin of animal multicellularity.

In Chap. 3, Ortega-Hernández highlights the importance of the fossil record to reconstruct the biology of extinct organisms and to understand how their morphology evolved over time. The discovery of new deposits with exceptionally preserved soft tissues and the application of new techniques to extract information from fossils are the drivers of discovery in animal palaeontology today. They have enabled the assignment of enigmatic fossils to their extant animal lineages, thus revealing crucial insights into the gradual assembly of the body plans of major animal groups (e.g. arthropods), as well as into the evolution of key animal features, such as the nervous system, limbs, and guts.

To begin the part “The Developmental View of Animal Evolution”, Kuo reviews the historical roles of comparative embryology for our understanding of animal evolution in Chap. 4. Even though it was long recognised that new forms originate by changes in development, the early studies on comparative embryology performed a more circumstantial role, mostly as evidence for identifying animal relationships. With the rise of molecular phylogenetics and developmental genetics, however, this role has been transformed into the field of EvoDevo, which is becoming a major framework to reveal the mechanistic causes for developmental and evolutionary changes in animal morphology.

Since embryonic development is a complicated process, not all changes are equally possible. A misplaced cell division or gene activation can lead to the death of the embryo. How can embryos change without generating abnormalities that affect the fitness of the individual? In Chap. 5, Genikhovich addresses this question by examining in detail the known and novel mechanisms by which developmental programs evolve, such as *cis*-regulatory changes and the rewiring of genetic

networks. Some of the discussed mechanisms constitute the basis for the evolution of morphological novelties—the topic of the next chapter.

Although evolutionary novelties can sometimes be evident, such as the turtle shell or insect wings, for most cases it is not something straightforward to determine. In Chap. 6, Almodí and Pascual-Anaya use a conceptual distinction between novelty and innovation to dissect what morphological novelties are, how they arise, and the developmental basis for their evolution, all under the light of the current findings in molecular and developmental biology.

The following two chapters describe how the comparative approach is bringing a fresh view into the evolution of two distinguishing features of animals—the embryonic germ layers and the nervous system.

The first embryological studies already recognised that embryonic tissues are divided into two or three primordial layers and that their specification is crucial for the development of the embryo. However, until recent years the factors and mechanisms controlling germ layer formation remained largely unknown. In Chap. 7, Wijesena discusses recent discoveries in cnidarians (e.g. sea anemones), a key group to understand the transition from two to three embryonic germ layers during animal evolution.

Animals are notorious for the ability to sense and interact with the environment in complex ways. This interaction occurs through sensory cells, specialised organs, and a centralised signalling network with peripheral nerves and a brain—the nervous system. How did such complex system evolve during animal evolution? In Chap. 8, Layden tackles this long-standing question from a developmental and functional perspective, revealing recent findings that challenge the widely accepted view that the nervous system evolved only once in the metazoan lineage.

Chapter 9 opens the part “The Genomic View of Animal Evolution” approaching a highly debated topic in biology—the relation between micro- and macroevolution. By considering the novel genomic properties uncovered in recent years, such as 3D organisation, Irimia and Maeso discuss the role of genomic changes in macroevolution, and if such changes can drive macroevolutionary processes. They propose that it is the expansion of regulatory potential in the genome that is the crucial factor underpinning macroevolutionary change.

Despite being relatively new, gene regulatory networks have become a central framework for understanding embryonic development. In Chap. 10, Sadier reviews their properties, logic, and how gene regulatory networks orchestrate morphogenesis. The ability to sequence transcriptomes of a wide range of species is vastly improving the resolution of these gene regulatory networks and is revealing the various ways they can drive or buffer morphological changes throughout animal evolution.

The part “Theoretical Approaches to Animal Evolution” begins with Chap. 11 where Melo explores the importance of modularity to understand the genotype–phenotype map. Most traits do not evolve independently. Shared regulatory kernels or developmental programs between traits of the same individual can significantly influence (enabling or constraining) morphological evolution. Recent efforts to clarify this interdependence based on quantitative trait loci studies and mathematical

modelling suggest that modularity is a key principle to understand the origin of variation within populations during the evolution of new phenotypes.

Computational modelling is becoming a major framework for biological research and the ultimate question for developmental biologists is straightforward—can we compute the embryo? In Chap. 12, Marín-Riera and Brun-Usan discuss the recent approaches to model and simulate morphogenesis, how they overcome the limitations of gene regulatory networks by better representing the dynamics and complexity of developmental processes, and what we can learn from computational biology when it comes to testing hypotheses and understanding the basis of phenotypic variation.

Finally, to conclude the part “Theoretical Approaches to Animal Evolution” and this book, Baedke revises in Chap. 13 the concept of biological individuality based on the recent findings of metagenomics and microbiome research. In spite of the intuitive sense, the definition of a biological individual is a complex and widely debated concept. The subject, however, acquired a new dimension with the discovery that animals host an incredible amount of microbial life, challenging our previous understanding of individuality and giving space to novel concepts, such as the holobiont as unit of biological organisation.

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We hope that by editing this book, we managed to deliver a comprehensive and updated picture of animal evolutionary developmental biology that can serve both as a first step into this fascinating field and as an inspiring source for new innovative studies in animal evolution.

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